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Green beards and master genes

There is a sense in which gene expression can be hierarchical: some genes are "master genes" that control the expression of many other genes. In other words, they select which genes to express when. It is thus entirely possible, and indeed in advanced organisms common, for a genome to encode a wide variety of phenotypes, only some of which get expressed, depending on the alleles of the master gene(s), on environmental cues, or both. Master genes can control gender, sexual orientation, and a wide variety of other complex structures and behavioral tendencies encoded for by complex assemblies of genes.

The green beard effect occurs when linked genes produce all three of the following: (1) a signal, (2) recognition of that signal in others, and (3) different behaviors (e.g. altruism) towards those exhibiting that signal. If the genes can remain linked, organisms expressing the green beard allele can cooperate with each other and spread in the population. Most evolutionary biologists, studying the genetic evolution of behaviors in animals, have tended to dismiss green beard effects as rare, because they have only rarely been unambiguously observed in the field, and because it's highly unlikely that genes can remain linked in this manner during sexual recombination.

I strongly suspect that this view is mistaken. It's hard to distinguish green beard from normal ("blue beard") signalling and recognition systems (such as those involved in kin altruism, mother/fetus interfaces, sexual selection, gender recognition, etc.) Green beard effects usually evolve "parasitically" on already existing "blue beard" signalling systems. Both of these make it difficult to recognize green beard effects, because they are usually strongly associated with existing "blue beard" signalling systems. Furthermore, strong linkages are not nearly as rare as has been assumed, because of the existence of master genes that control the expression of many other genes. Alternative alleles of a master gene could, for example, code for the selective expression of alternative strategies encoded in many other genes. In other words, a wide variety of genes, each existing in all members of a species, could code for two or more complex strategies, with a master gene coding for *which* of the strategies actually gets expressed.

Nature provides a great example where I believe a master green beard gene is at work: the side-blotched lizard. The male lizards have three different strategies for defending mates: dominance, sneakiness, and cooperative mate guarding. Violating standard theory, these sexual strategies correspond to very distinct throat color patterns: orange, yellow, and blue. Orange-throated lizards dominate a mate and territory and don't cooperate with other males in this task. Yellow-throated lizards look and act like females, and sneak around cuckolding orange-throated lizards. Blue-throated lizards cooperate to detect and fend off yellow lizards, but are weaker and

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Nick Szabo

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can be defeated by yellow-throated lizards. The result is

> a kind of "rock-paper-scissors" game, where orange defeats blue, blue defeats yellow, and yellow defeats orange. The result is an evolutionarily stable situation in which no single color morph can dominate the population...
>
> The remarkable thing about the color morphs of side-blotched lizards is that an enormous range of behavioral, physiological, and life-history traits are correlated with throat color. Genes for different traits can be linked physically if they occur close together on a chromosome, but according to [evolutionary biologist Barry] Sinervo, throat color is linked to far more traits than could possibly be physically linked on the same chromosome.
>
> It's almost as if the whole genome is tightly tethered to this one master locus," he said. "In order to be a really 'good' blue, you have to have all these other alleles [of different genes] lined up in the right combination, and the same is true for orange and yellow color morphs. So there is strong selection for these different fitness combinations.
>
> "The whole genome crystallizes into three types," Sinervo said. "The alleles for all these different traits should be independent and separated on the chromosomes, yet the genes are interacting through this one locus."

The lizards, the throat color gene determining orange, yellow, or blue throat splotches seems to be tightly correlated to the rest of a distinct complex strategem. This is inexplicable by traditional arguments against the green beard, which assume that the alternative strategies are coded in three separate sets of alternative alleles, all of which must be expressed to work. Being broken up and recombined every generation, they cannot stably evolve as distinct and competing sets of genes. But the cooperation of the blue-throated lizards qualifies as a green beard effect, bringing this assumption into question. The linkage of throat colors with complex behavioral strategies can be readily explained if *all three* strategies are encoded in *all* male side-blotched lizard genomes, and there is only one strong linkage, that is between the throat color gene and a gene that controls the expression of many other genes. Indeed, I wouldn't be surprised if the throat color gene and the master gene were the same gene.

There are strong adaptive reasons for master genes to control complex assemblages in this way. Behavioral strategies, and indeed structures and metabolic pathways, that are too complicated but not ubiquitous in a breeding population are encoded across too many unlinked genes. As a result they cannot survive sexual recombination. All advanced multi-cellular organisms thus have master genes or distinct chromosomes that control the expression of many other genes. In the case of gender, distinct chromosomes are usually involved, but master genes can behave similarly, producing small sets of complicated strategies, each strategy very distinct from each other and each a distinct alternative to the other. In information theory terms, there is a large information distance between each of the alternative strategies, just as there are many differences between the genes expressed in the development of a female versus those expressed in a male. A wide variety of distinct morphological and behavioral traits are bundled into a small number (in the case of genders, typically two) of alternatives. A wide variety of other genes encode the distinct complex structures or strategies, to be invoked by master genes, developmental stages, and environmental cues. Since the complicated parts of each strategy are encoded in *every* member of the breeding population, there is no problem with sexual recombination breaking linkages between many genes encoding each strategy: each gene of each strategy is still there waiting, in the next generation, to be invoked by the master gene.

I strongly suspect that master genes and green beard effects analyzed in this manner will shed light on a wide variety of puzzles in evolutionary biology, including sexual selection, sexual orientation, and racial and ethnic preferences that, under the assumption that green beard effects are not important, have long defied analysis or been assumed to be purely environmental.

Posted by Nick Szabo at 2:13 PM

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